Ann. Natal Mus. Vol. 32 Pages 149–162 Pietermaritzburg October, 1991

Afrotropical Asilidae (Diptera) 21. Observations on the biology and immature stages of *Damalis femoralis* Ricardo, 1925 (Trigonomiminae)

by

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ABSTRACT

Various aspects of the biology of the grassland asilid *Damalis femoralis* Ricardo are described and discussed, including prey capture, prey preferences, mating, and oviposition. The egg and first larval instar are described and compared with those known for other asilids. The importance of these predatory flies in grassland ecology is briefly discussed.

INTRODUCTION

Robber flies of the family Asilidae constitute one of the largest and most commonly encountered groups of flies. The family as a whole, distributed throughout the world, is arguably the most important group of insect predators known. Although many species are large and conspicuous it is surprising how little is known about Afrotropical representatives. While the taxonomy of Afrotropical asilids, although far from complete, has received, and is currently receiving, adequate attention, virtually nothing is known about their biology and the important role they must play in insect ecology.

In a preliminary study of the biology and immature stages of *Neolophonotus dichaetus* Hull (Londt & Harris 1987) I briefly surveyed our limited knowledge of Afrotropical asilid biology; at that time confined to a few published prey records and superficial comments on habitat preferences. Although a little more biological information is now available, this is limited to two conference abstracts relating to general observations on prey preferences (Londt 1987 1990) and some interesting observations made on the predatory behaviour of a few species (mainly *Neolophonotus*) which feed on spoonwinged Nemopteridae in the south-western Cape Province (Picker, Leon & Londt 1991). Excluding the present study the most complete published biological study of an Afrotropical asilid remains the preliminary work on *N. dichaetus*, an apocleine species with unique oviposition behaviour and interesting first instar larva.

During efforts to assemble as much material as possible for museum based taxonomic studies I have spent much time in the field collecting African Asilidae. During a few of my expeditions, some organised especially to gather *Damalis* material for a taxonomic revision of this genus (Londt 1989*a*), I became aware of the potential for more detailed biological research offered by the trigonomimine species *Damalis femoralis* Ricardo and some of its congeners. Not only is the period of adult activity of this species highly predictable but it is short, allowing fairly intensive work to be done in a relatively short time. In addition the population density of this grassland asilid is often remarkably high and, with a little experience, suitable situations for their existence are easily recognised.

MATERIALS AND METHODS

Comments on seasonality are based on museum specimen labels and field experience. Information regarding prey preferences has been gathered fairly randomly over a number of years, although one short trip to Royal Natal National Park (R.N.N.P.) between 7–11 April 1990 was undertaken with the prime objective of learning as much as possible about this and other aspects of the biology of *D. femoralis*. Some material from the R.N.N.P. trip was brought back to the laboratory in Pietermaritzburg for identification, counting and analysis; all prey items being preserved and deposited in the Natal Museum for future reference. The eggs and larvae recovered from a single female specimen from R.N.N.P. were subjected to scanning electron microscopy; both eggs and larvae being placed, living, on stubs, and gold coated. Other more specific materials and methods used are more appropriately described under the relevant sections which follow.

RESULTS AND CONCLUSIONS

General biological features

D. femoralis has as yet not been collected outside the province of Natal where adults are active between January and April (Londt 1989*a*). My impression is that populations are at their peak at the end of March and beginning of April. Adult activity appears to terminate with the onset of cooler weather which usually occurs before the end of April. As yet there are no May records for the species.

D. femoralis is usually encountered in tall grass. While often found adjacent to indigenous forest patches the species appears to prefer gullies, depressions or the lower parts of small valleys rather than more exposed situations. The study site at R.N.N.P. is pictured in Fig. 1. This depressed, grassy site, adjacent to a pine plantation, is situated immediately alongside the Mahai Caravan Park. A small perennial stream, running down between the plantation and study area, and overhung by long grass, drains the area.

Preliminary efforts to establish daily activity rhythms (during the first week of April) indicate that adults overnight clinging to grass stalks. Short, slow flights began at about 07:30. At this time individuals flew only when disturbed and often retained the wings in a partially extended condition after landing. By 08:00 individuals flew 'on their own initiative'. Feeding individuals were first encountered from about 09:00 and foraging appeared to continue throughout the day although there seemed to be mid-morning and late afternoon peaks in this activity. Mating pairs were encountered from about 10:00 and mating too appeared to take place throughout the day; a possible peak in this activity appeared to take place during the early afternoon (14:00–15:00). Flight became sluggish once the sun had set and the air had become cooler (*ca* 17:00) and all activity ceased with nightfall.

Although I did not actually witness predation of *D. femoralis* by other creatures it seems likely that they may fall victim to a variety of insect predators. During

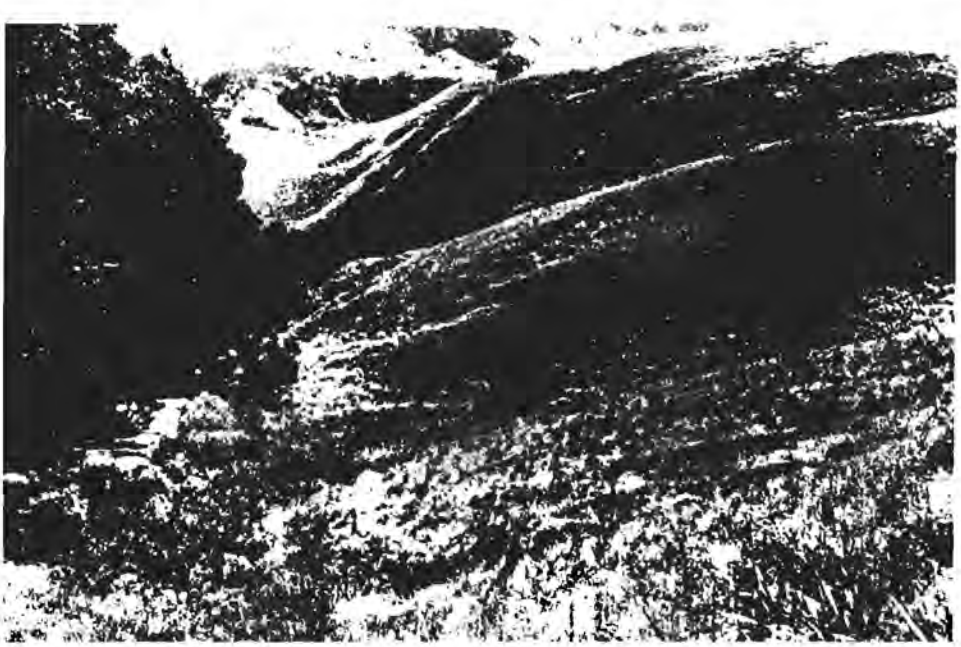


Fig. 1. The Royal Natal National Park study site where *Damalis femoralis* Ricardo was abundant during April 1990.

work at R.N.N.P. I encountered at least three species of assassin bugs, a number of large spiders, various mantids and at least two species of dragonfly (*Trithemis dorsalis* (Rambur) & *Chlorolestes fasciata* (Bermeister)) apart from two other asilid species (*Dasophrys fortis* Londt & *D. dorattina* Londt) large enough to prey on *D. femoralis*.

Prey capture

Prey capture was witnessed on only a few occasions. In each instance the asilid was perched on a grass stalk when it first noticed the prey. The foraging asilid darted directly at the passing prey item, captured it, and returned to a perch to feed. During a mass dispersal flight of alate ants one asilid was seen to rise some 3–4 metres into the air in pursuit of an ant (which it failed to capture). Although individuals, especially males, were commonly seen participating in long, meandering flights it is not known if these were foraging or mate seeking flights. For the present the latter is believed to be more likely (see below).

Prey preferences

Ninety-three individual prey records, gathered at seven localities over a period of a few years, are available for analysis (Table 1). The largest single period sample is 43 prey items from R.N.N.P. collected between 7–11 April 1990.

All known prey items are winged insects and a taxonomic analysis at family level, where possible, appears in Table 2. Hymenoptera form the bulk of existing

TABLE 1

An analysis by orders of prey insects captured by *Damalis femoralis* Ricardo at seven different localities (1 = Royal Natal National Park, 2 = Loteni Nature Reserve, 3 = Cathedral Peak, 4 = The Kop, Kranskop, 5 = Normandien Forest Reserve, 6 = Umtamvuna Nature Reserve, 7 = Nkhandla Forest Reserve). * = More than a single collection period.

	Localities (see caption)							
Order	1*	2*	3	4*	5	6	7	*Total*
Hymenoptera	42	4	5	3	—	1	—	55
Hemiptera	4	5	1	3	—	—	1	14
Diptera	3	2	3	1	1	—	—	10
Coleoptera	4	3	2	—	—	—	—	9
Psocoptera	3	—	—	2	—	—	—	5
Total	56	14	11	9	1	1	1	93

TABLE 2

Prey of *Damalis femoralis* Ricardo identified to family level.

Order	Total	%	Family	No.	%
Hymenoptera	55	59,1	Formicidae	49	52,7
			Platygastridae	2	2,2
			Halictidae	1	1,1
			Ichneumonidae	1	1,1
			? Torymidae	1	1,1
			?	1	1,1
Hemiptera	14	15,1	Cicadellidae	6	6,5
			Lygaeidae	5	5,4
			Aphididae	1	1,1
			Miridae	1	1,1
			? Anthocoridae	1	1,1
Diptera	10	10,8	Empididae	3	3,2
			Chloropidae	1	1,1
			Culicidae	1	1,1
			Phoridae	1	1,1
			Sphaeroceridae	1	1,1
			Tipulidae	1	1,1
			? Lauxaniidae	1	1,1
			?	1	1,1
Coleoptera	9	9,7	Staphylinidae	6	6,5
			? Scarabaeidae	1	1,1
			?	2	2,2
Psocoptera	5	5,4	Peripsocidae	3	3,2
			Ectopsocidae	1	1,1
			Psyllipsocidae	1	1,1
Total	93	100,1			

records with alate Formicidae dominating to the extent of representing 52,7 % of all data. Field observations, however, suggest that this is a distortion of the truth as many of these records (37) were collected during a few hours at R.N.N.P. when alates of one particular ant (*Solenopsis* sp.) were taking part in mass dispersal flights. During this period three other asilid species (*Dasophrys dorattina*, *Rhabdogaster nuda* Loew and *Neomochtherus* sp.) were also found feeding on these ants. There is no doubt that alate ants are very acceptable as they are amongst the largest, and probably easiest, of prey items susceptible to capture by *D. femoralis* (see below), but as these are not always readily available, ants cannot be accepted as the main dietary component. Although there does not appear to be a significant difference between the types of insects taken by male and female *D. femoralis* (Table 3) females appear to be better able to capture larger prey than males (see below) although measurement of 31 *D. femoralis* specimens (part of the community survey shown in Fig. 4) indicates that males, unlike the situation in many other asilid species, are generally a little larger than females (Table 4).

TABLE 3

A comparison of prey taken by males and females of *Damalis femoralis* Ricardo.

Prey identification (Order)	Female No.	Female %	Male No.	Male %	Total No.	Total %
Coleoptera	4	7,3	5	13,2	9	9,7
Diptera	3	5,5	7	18,4	10	10,8
Hemiptera	8	14,5	6	15,8	14	15,1
Hymenoptera	37	67,3	18	47,4	55	59,1
Psocoptera	3	5,5	2	5,3	5	5,4
Totals	55	100,1	38	100,1	93	100,1

TABLE 4

Size comparison, as expressed by Length × Depth measurements, of male and female *Damalis femoralis* Ricardo collected during a community study at Royal Natal National Park.

	Females	Males	Total
Count	14	17	31
Mean L×D	33,5	36,6	35,2
Min L×D	26,1	28,0	26,1
Max L×D	40,8	48,1	48,1

The wide range of acceptable prey suggests that *D. femoralis* is a general feeder, accepting a wide variety of prey. An attempt was made at R.N.N.P. to establish exactly what prey was available in order to assess just how catholic is the diet of this grassland asilid. This was done by sweeping an area in which *D. femoralis* was abundant and analysing the entire catch. In Table 5 a taxonomic breakdown of the community sample is presented alongside all available prey data for the same locality (n = 56). Although Hymenoptera comprise the bulk of prey (data distorted by dispersing alate ants as explained above) it is clear that certain groups of organisms are apparently not, or little, utilised by *D. femoralis*. In each instance, however, there are good reasons for their unsuitability. Firstly it appears that only flying prey items are acceptable and this therefore excludes all spiders (Araneae) as well as larval or nymphal insects (eg. all but one of the Lepidoptera

TABLE 5

A broad taxonomic breakdown of the community of which *D. femoralis* is part at Royal Natal National Park and data regarding prey actually captured by this asilid at this locality.

	Grassland community (April 1990)		*D. femoralis* prey (all R.N.N.P. records)	
Order	No.	%	No.	%
Araneae	40	11,2	—	—
Coleoptera	9	2,5	4	7,1
Diptera	84	23,6	3	5,4
Ephemeroptera	1	0,3	—	—
Hemiptera	86	24,2	4	7,1
Hymenoptera	85	23,9	42	75,0
Lepidoptera	9	2,5	—	—
Mantodea	5	1,4	—	—
Odonata	1	0,3	—	—
Orthoptera	22	6,2	—	—
Psocoptera	3	0,8	3	5,4
Thysanoptera	11	3,1	—	—
Total	356	100,0	56	100,0

sampled were caterpillars) as well as fully developed apterous insects (eg. worker and soldier ants). Secondly as size of prey appears to be important, the larger Orthoptera, Lepidoptera, Mantodea and Odonata, all as big or bigger than *D. femoralis* were certainly too big for the asilids to capture. Conversely the tiny Thysanoptera may have been too small.

The size range of prey taken by *D. femoralis* was examined in greater depth by measuring the maximum length and depth of all available prey items as well as of all the invertebrates collected in the R.N.N.P. community sample described above. As asilids probably assess the suitability of a prey item by visually gaining an overall impression of its bulk it was decided to multiply the length measurements by those of depth (the L×D value referred to below). In this way an indication of the range of prey taken by *D. femoralis* was obtained along with comparative information about the prey capturing abilities of both males and females (Fig. 2). As there were six broken prey items which could not be properly measured the total sample size was 87. The smallest prey item had a L×D value of 0,4 while the largest was 12,9. Although the prey capturing abilities of males and females were similar, all but one of the prey items with a L×D value in excess of 6 (13 in all) were taken by females; suggesting that females are able to catch larger prey than males. Of interest is the fact that alate ants were amongst the larger of the prey items taken (Fig. 3). The size range occupied by *D. femoralis* itself within the R.N.N.P. community is shown in Fig. 4. It is clear that it accounts for much of the minor peak evident between L×D groups 9–17. The prey of *D. femoralis*, having L×D values between 0,1–13,0 (Fig. 2), would clearly form part of the community which would normally occupy the first three L×D groups shown in Fig. 4 (ie. some of the smallest creatures in the community).

Of the 93 prey records available no fewer than 55 (59,1 %) are for female *D. femoralis* in comparison with 38 (40,9 %) for males. This kind of sexual differ-

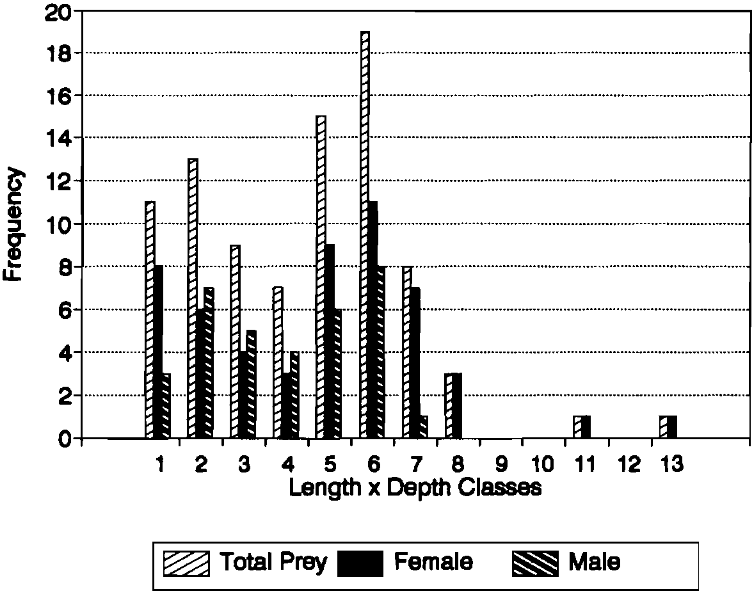


Fig. 2. The size range of prey items captured by *D. femoralis* Ricardo with a comparison of prey captured by males and females. L×D Classes in units of 1 ie. Class 1 = L×D values between 0,1–1,0, Class 2 values between 1,1–2,0 etc.

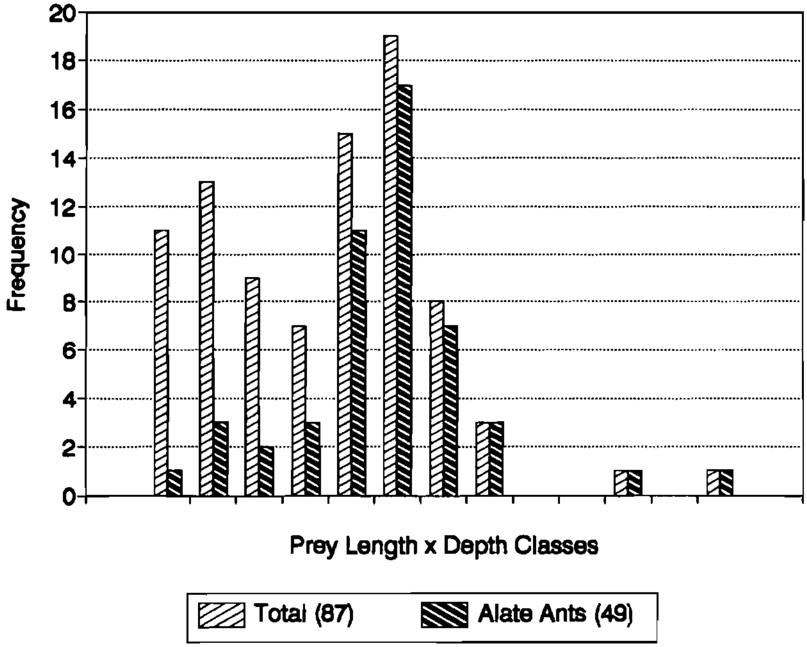


Fig. 3. The size range of prey items captured by *D. femoralis* Ricardo, showing that alate Formicidae were among the largest of prey items taken. L×D Classes in units of 1 ie. Class 1 = L×D values between 0,1–1,0, Class 2 values between 1,1–2,0 etc.

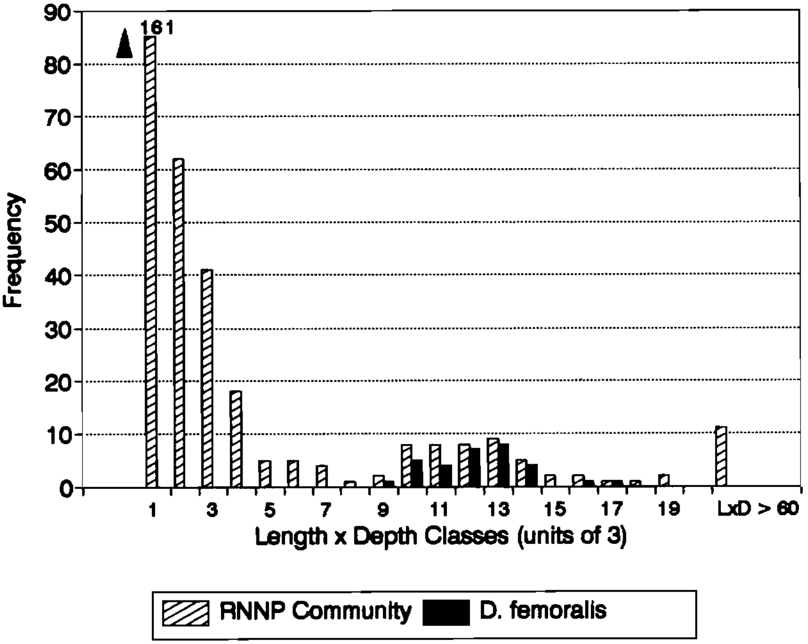


Fig. 4. The size ranges of invertebrates in the grassland community at Royal Natal National Park, showing that part of the range occupied by *Damalis femoralis* Ricardo. L×D Classes in units of 3 ie. Class 1 = L×D values between 0,1–3,0, Class 2 values between 3,1–6,0 etc.

ence has been noted by many authors and appears to be reasonably consistent. For example my own data-base (comprising some 800 prey records for all species of Afrotropical asilids) shows an overall 64 % : 36 % ratio for females and males respectively (see also Londt 1990). As male and female *D. femoralis* do not differ greatly in size, the most obvious explanation for this sexual difference is that the females require to feed more frequently than males. As another possible explanation is that there may be more females than males in the population, I conducted a simple sampling experiment at R.N.N.P. I captured 100 individuals at random and sexed them, the result was 44 females and 56 males, suggesting that there are more or less equal numbers of males and females in the population. The fact that there were slightly more males than females may be because males are more active than females, and would probably have been more commonly observed during the sampling period.

Mating

Field observations suggest that males are generally more active than females, flying for longer periods and ranging over greater distances. The sustained flight of males is also highly erratic, individual males weaving in and out of the vegetation, apparently in search of females. Males encounter either perched or flying females; if the latter they immediately pursue the female at a following distance of about 20 cm until the female alights on a grass stalk. Having located a perched female the male hovers about 10 cm below her for a period of about five seconds. During this period the male usually aligns his body so that the abdomen points towards the female's grass stalk (ie. the male faces in the opposite direction to the female). Without any apparent invitation the male very rapidly swoops upward, simultaneously turning ventral side upward, and encounters the female. In a sequence of movements too rapid to record without high-speed photography, the male genitalia engage those of the female and his hind legs wrap around her, effectively immobilising her (Fig. 5). Once successfully united the male may release his hold on the female and either grasp the grass stalk, still in an inverted position, or release all hold on any substrate such that he hangs in midair behind the female. The female displays no obvious reaction to any part of the male's courtship performance and so, once he has relinquished his embrace, she may fly off, carrying the male with her (he flaps his wings to aid the tandem flight but she determines the direction taken), or she may continue with a meal commenced before the coupling (only one such instance was seen). A number of unsuccessful couplings were observed, the male and female apparently engaging in a brief tussle before separating.

The duration of copulation appears to be highly variable, some pairs remained together for as little as a few seconds while one pair was timed at over 10 minutes.

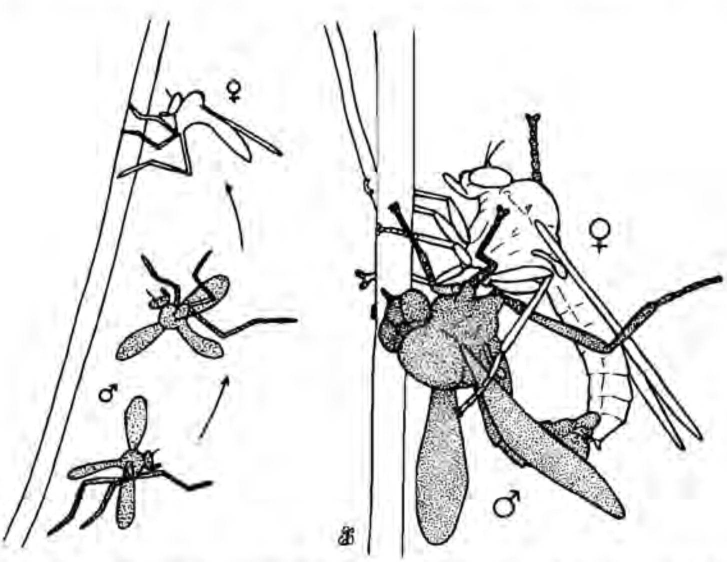


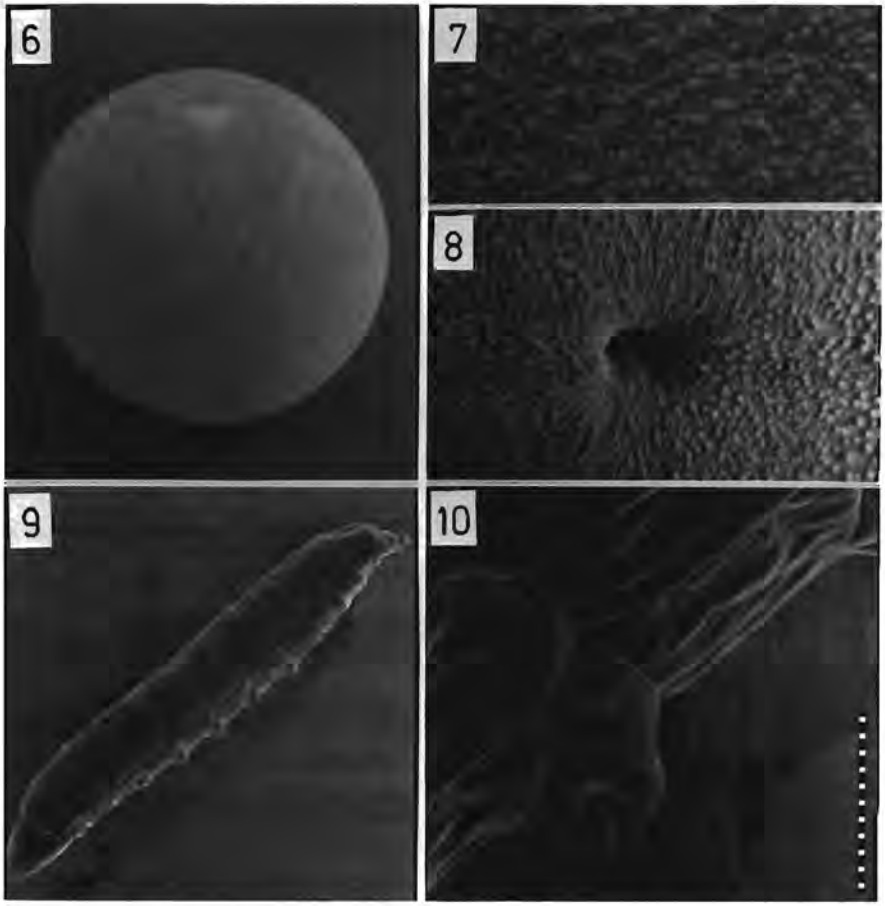
Fig. 5. Copulation in *Damalis femoralis* Ricardo. Left: male hovers below female before swooping upwards toward her (diagrammatic). Right: male encountering female (drawn from colour transparency).

Oviposition and the eggs

Females, which possess unspecialised ovipositors appear to display generalised oviposition behaviour and it is believed that the eggs are shed at random and merely allowed to fall to the ground or into the, often thick, grassy ground-cover.

The only information on fecundity available was obtained from a single gravid female, which was placed in a plastic vial and left to die. This female laid no fewer than 326 eggs of which a great proportion hatched.

The eggs are creamy white in colour and almost spherical (Fig. 6), measuring 0,32 mm in diameter (mean of 10 measured eggs). The chorion appears smooth under the low magnifications of a stereo-microscope but is evenly covered with tiny spicules when viewed with the SEM (Fig. 7). The only external feature of special note is a single pore-like opening (Fig. 8) which is probably a micropyle. Although I have not undertaken an exhaustive survey of the published work on asilid eggs, I am only aware of one report of the existence of a micropyle and this was for the Nearctic *Eudioctria tibialis* Banks (Scarbrough 1981). Although the detailed work of Melin (1923) on a variety of Swedish asilids and the brief review of eggs provided by Lavigne, Dennis & Gowen (1978) make no mention of micro-



Figs 6–10. *Damalis femoralis* Ricardo. 6–8. Egg. 6. Entire. 7. Surface spicules. 8. Micropyle. 9–10. First instar larva. 9. Entire. 10. Pseudopod. Scale line = 6: 136μm 7–8: 7,5μm 9: 0,27μm 10: 30μm.

pyles, few people have subjected eggs to detailed scrutiny using scanning electron microscopy. While most asilid eggs appear to be broadly oval to elongate-oval, as is the case with *N. dichaetus*, subspherical eggs have been reported for *Leptogaster cylindrica* (De Geer) (Melin 1923), *L. flavipes* Loew (Scarbrough & Sipes 1973) and *Smeryngolaphria pallida* Bromley and *P. bromleyi* Londt (Londt 1989*b*). These species mostly inhabit vegetation in grassland or scrubland situations and, like *D. femoralis*, lack specialised ovipositors, suggesting that spherical eggs may be common to all such species.

Incubation and eclosion

Eggs laid by the single female mentioned above began hatching 14 days after her confinement. As it was not noted when the first eggs were laid a precise incubation period cannot be given. As it is believed that the female could have commenced laying almost immediately, it is possible that incubation may be as long as 14 days.

First instar larva

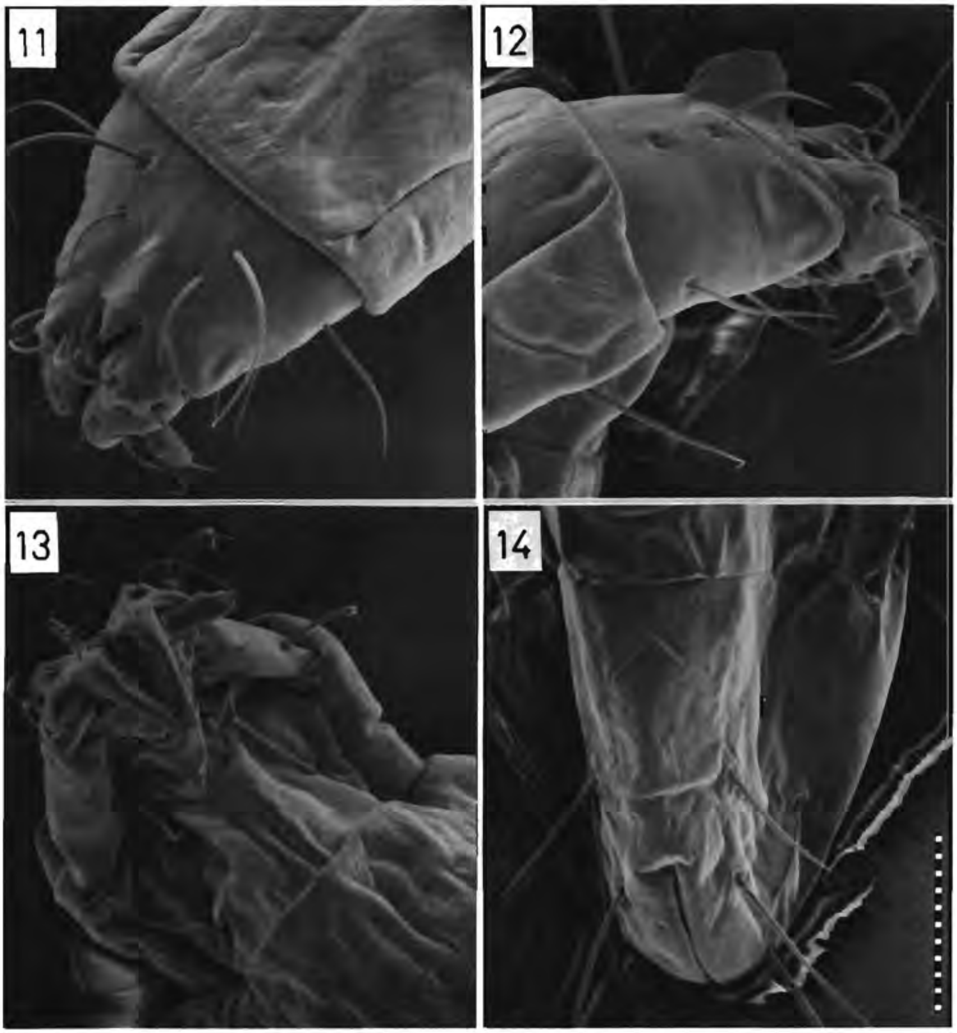
Larva (Fig. 9) white, elongate, subcylindrical, tapering at each end, and measuring *ca* 1 mm long and *ca* 0,13 mm wide. In general appearance similar to *N. dichaetus*.

Head (Figs 11–13): Anterior process or egg burster well developed and clearly keel-like (broader in *dichaetus*). Antenna poorly defined and hardly protruding from the cranium (protruding and subspherical in *dichaetus*). Ventral aspect of head membranous and lacking spatulate setae (ventral plate and spatulate setae present in *dichaetus*). Maxillae somewhat bulbous dorsobasally (not so in *dichaetus*); palpi similar to *dichaetus* but shorter. Labium small, papilla-like, lacking pits and setae as found in *dichaetus*. Cranial and other setae similar in position, but not development, to *dichaetus*; anterior cranial setae, at base of egg burster, between antennae, well developed (tiny in *dichaetus*); lateral cranial seta (behind antenna) well developed (absent in *dichaetus*).

Thorax: Unremarkable, similar to *dichaetus*; each segment bearing a single pair of long ventrolateral setae (probably assist in locomotion).

Abdomen: 9 segmented as in *dichaetus*. A pair of anteroventral, contractile pseudopods (locomotory pads) (Fig. 10), lacking spines, setae or crotchets, situated on segments 2–6 (Fig. 9) (*dichaetus* has pseudopods on segments 2–7); segments 1 and 7 lacking pseudopods. Segments 8 and 9 closely associated, appearing like a single terminal segment; with two pairs of long setae dorsally and ventrally as in *dichaetus*. Anus slit-like (Fig. 14), situated terminally (more ventrally situated in *dichaetus*).

Very little can be said about the larvae of *D. femoralis* apart from the fact that it, like *N. dichaetus*, also lacks pseudopods on the first abdominal segment. As mentioned in my paper on *N. dichaetus* the only asilids previously reported as lacking these particular pseudopods are members of the Leptogastrinae and the isolated instance of *Machimus rusticus* (Meigen) illustrated by Musso (1981). It



Figs 11–14. *Damalis femoralis* First instar larva. 11–13. Head capsule. 11: Dorsal. 12. Lateral. 13. Ventral. 14. Terminal abdominal segments, ventral. Scale line = 11 & 13: 38μm 12: 30μm 14: 43μm.

appears therefore that this phenomenon may be more common than previously suspected.

No effort was made to rear the larvae of *D. femoralis* and so no information is available on successive larval instars.

DISCUSSION

D. femoralis differs from *N. dichaetus* both morphologically and biologically; something to be expected as the two species belong to different subfamilies. The two species may indeed represent evolutionary extremes found in the family.

Although the necessary cladistic work has not yet been undertaken, I believe *Damalis* possesses a number of plesiomorphic features; its unspecialised feeding and oviposition supporting this contention. *Neolophonotus* is, on the other hand, one of the more highly specialised or apomorphic genera of the Asilinae; the elaborate oviposition behaviour described in my study of *N. dichaetus* adding weight to this belief (Londt & Harris 1987). As hardly any biological work on Afrotropical species has been done, we must await detailed comparative studies of the various asilid subfamilies from other zoogeographical regions. Until then students of the Afrotropical fauna will have to be content to undertake the basic research necessary to build on the limited knowledge presently available for this region.

Impact of *Damalis femoralis* on the grassland invertebrate fauna

The simple community survey undertaken at R.N.N.P. provides preliminary evidence for the considerable impact which *D. femoralis* must have on cohabiting invertebrates. Of the 356 invertebrate specimens representing the community at the study area, no fewer than 31 (ie. 8,7 %) were *D. femoralis*; a very dominant segment of the community. Although many other predators probably share the spoils with *D. femoralis* (the sample including 40 Araneae—most of which were quite small, 10 Empididae, 5 other Asilidae, 5 Mantodea, 2 Reduviidae and 1 Odonata) this species must surely have had the greatest impact.

Although a number of other asilids were collected within the study area at R.N.N.P., I do not believe that these compete directly for the same food resources. *Dasophrys dorattina* and *D. fortis* are normally associated with woody plants and so, although found close to the grassy situations dominated by *D. femoralis*, may not actively compete with this species. *Neomochtherus* sp., also found in the same grassy areas as *D. femoralis*, usually occurs at lower levels in the grass and so may also not actually be competing. *Rhabdogaster nuda*, while also found at higher levels in grass is usually associated with more elevated situations (ie. crests between depressions), while *D. femoralis* appears to prefer depressions.

ACKNOWLEDGEMENTS

I wish to thank the following for assistance rendered. Miss Shirley Chinn, Research Assistant, Department of Entomology, Natal Museum, patiently measured many specimens and assisted in their identification; Prof. Michael Samways, University of Natal, identified Odonata; Dr Hamish Robertson, South African Museum, identified Formicidae; Mr Vijay Naidoo, Electron Microscope Unit, University of Natal, scanned and photographed the asilid eggs and larvae; Mr Stan Bright, Natal Museum, produced photographic prints for publication; my colleagues Dr David Barraclough and Mr Andy Whittington commented on the manuscript; The Natal Parks Board supported my research by providing collecting permits. I acknowledge The Foundation for Research Development for financial assistance in the form of a grant in support of my research.

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Date received: 4 September 1990